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NOTES AND LITERATURE

PLANT CYTOLOGY

Some Recent Research on the Cilia-forming Organ of Plant Cells.—The blepharoplast, or cilia-forming organ of plants, is present in the sperms and other motile gametes and in the zoospores. When fully developed it lies close against the plasma membrane of the cell in the form of a granule or band of various shapes to which the cilia are attached. The origin of the blepharoplast has been the subject of considerable research with conflicting conclusions.

Strasburger in 1900 from studies on the zoospores of Œdogonium, Cladophora and Vaucheria decided that the blepharoplast arose in the plasma membrane (Hautschicht), the nucleus lying in close proximity at the time of its formation; Mottier later described a similar origin for the blepharoplast of Chara. In sharp contrast to the above conclusions are those of Belajeff from studies on the sperms of certain pteridophytes, Ikeno for Cycas and Marchantia, and Hirasé for Ginkgo, who hold that the blepharoplast is an attractive sphere or centrosome. Belajeff in particular has consistently described the blepharoplast as occupying, as a centrosome, the poles of the spindle in the mitosis previous to the formation of the sperm mother cells, and has held that the blepharoplasts of Marsilia came from centrosomes passed on from the previous mitoses; each sperm mother cell being thus supplied with a blepharoplast. Ikeno, especially from studies on Marchantia, also holds to the centrosome nature of the blepharoplast, but his conclusions are disputed by Miyake. A third group of investigators to which Davis and Yamanouchi also belong (as will be noted from the reviews which follow) have described the blepharoplast as arising in the cytoplasm while the nucleus is in a resting condition, and as holding no genetic relation to any preceding mitoses. Thus Webber from very thorough studies on the cycad Zamia described the blepharoplasts as developing *de novo* on opposite sides of the nucleus and at some distance from it before the mitosis that precedes the differentiation of the sperm nuclei; Shaw for Marsilia also claimed that the blepharoplasts did not occupy the poles of the spindle in the final mitosis, as would be expected of a centrosome-like body.

These divergent views have great theoretical interest in relation to the subject of the polar organization of cells reviewed in the July number of the NATURALIST. Zoospores invariably present a conspicuous polarity since their cilia are situated at one end or at a definite point on the side, and while the complex coiled structure of many sperms obscures this polar organization the process of blepharoplast development is always from a region which is clearly a pole of the cell. Indeed, these types of cells present some of the best illustrations of complex polar organization. Perhaps the most vital problem of zoospore formation and spermatogenesis is then the question whether or not the polar organization of these cells arises *de novo* at the time of their development or is handed on from the succession of cells which are their progenitors.

Davis[1] found in the zoospores of Derbesia a very interesting subject for the study of a remarkable blepharoplast. Derbesia is a marine green alga in the group of the Siphonales, distinguished from other forms in the same group by having very large zoospores, each of which is provided with a circle of numerous cilia. These zoospores are developed in a large sporangium which contains at first several thousand nuclei, but a process of nuclear differentiation begins very shortly in the young sporangium; certain of the nuclei increase in size while the great majority begin to degenerate and finally break down. The large surviving nuclei become distributed rather uniformly throughout the protoplasm of the sporangium, and each is evidently the center of dynamic activity for the cytoplasm in its vicinity. This is indicated by the arrangement of numerous conspicuous protoplasmic strands which radiate from the nucleus between the surrounding plastids.

The segmentation of the protoplasm does not begin until the process of nuclear degeneration is practically ended, and the sporangium contains only the larger nuclei (from 30–300), which are to take part in spore formation. Cleavage furrows start from the periphery of the sporangium and cut into the protoplasm in the form of curved and branching furrows.

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[1] Davis, B. M. Spore Formation in Derbesia. *Ann. of Bot.*, XXII, p. 1, 1908.

These at first mark out large areas, which, however, become successively smaller as new furrows are formed at the periphery or strike off from the sides of the older ones. Finally the protoplasm of the sporangium becomes divided into approximately equal masses around the large surviving nuclei. These masses are the zoospore origins and each develops into a uninucleate zoospore.

The nucleus first lies at the center of the zoospore origin, with protoplasmic strands radiating out in all directions among the plastids. Granules are present at the bases of the protoplasmic strands close to the nuclear membrane. The nucleus then moves somewhat towards the periphery of the cell and it becomes clear that the protoplasmic strands on that side at least actually extend to the plasma membrane; these strands become arranged in the form of a funnel with the broader end against the plasma membrane. With this stage the zoospore origins clearly exhibit a polar organization.

A circle of granules, which is nearly twice the diameter of the nucleus, now appears where the broader region of the funnel-shaped arrangement of strands meets the plasma membrane. From earlier stages it seems probable that these granules pass along the strands as organized bodies from the neighborhood of the nucleus; they certainly arise within the cytoplasm. The granules in the circle finally fuse with one another to form a firm ring, which lies in the plasma membrane or just under it; this ring is the belpharoplast. The blepharoplast later splits into two rings, one immediately below the other, and the circle of numerous cilia grows out from the lower. The nucleus finally returns to a position near the center of the cell.

The most important points to be noted in this history of the origin of the blepharoplast in Derbesia are as follows. *First,* it seems clear that the nucleus is concerned in a most intimate manner with the development of the blepharoplast, since the numerous granules, which form the ring, appear to come from near the surface of the nucleus and travel along the radiating strands arranged in the form of a funnel; the elements forming the blepharoplast are not developed in the plasma membrane. *Second,* these very numerous granules can not be centrosomes and bear no relation to mitotic figures for there are no nuclear divisions in the sporangium. *Third,* the polar organization of the maturing zoospores does not appear to be present in the younger stages when the nucleus occupies a central position in the zoospore origin.

Yamanouchi[2] has given an account of spermatogenesis for Nephrodium in one of a series of papers dealing with the life history and apogamy of this fern. The blepharoplasts arise *de novo* just before the last mitosis in the antheridium, that mitosis which differentiates the sperm mother cells. They are first seen as small bodies lying within the cytoplasm on opposite sides of the nucleus and at a considerable distance from it; they appear suddenly, as differentiated by staining, and are unexpectedly large. The blepharoplasts move towards the nucleus and during the final mitosis take positions near the poles of the spindle. Sometimes the blepharoplasts may lie exactly at the poles of the spindle, and consequently suggest relationships to a centrosome, but this is not often, and there can be no such relationship in Nephrodium because centrosomes are not present in the earlier mitoses of the antheridium or at any other period of the life history.

As a result of the final mitosis in the antheridium each sperm mother cell receives one of the two blepharoplasts close by the side of the daughter nucleus. The nucleus in the sperm mother cell now increases in size and the blepharoplast, at first spherical, changes its form. It enlarges and is flattened somewhat against the side of the nucleus and begins to elongate. The outline becomes at first rhomboidal and then band-shaped as the blepharoplast gradually extends around the nucleus in the form of a semi-circular band.

A complicated development follows for both the nucleus and the blepharoplast. One end of the blepharoplast grows wedge-shaped and is loosely applied to the nucleus while the other end remains pointed and extends around in very close contact with its surface. The nucleus meanwhile changes its form, becoming a coiled structure and the elongating blepharoplast follows the coils in the form of a narrow band, which reaches to the end of the nucleus, and finally by extensive lateral growth covers the coil. In this manner the coiled and spiral form of the sperm is developed, and by this time numerous cilia have grown from the surface of the blepharoplast.

There is another structure in the sperm mother cell which must be briefly described. It appears as a minute body in the situation previously occupied by the central spindle of the final mitosis, and consequently far removed from the blepharoplast, which lies near the polar region of the spindle, with the nucleus between them. This structure is the "Nebenkern" of other authors. The "Nebenkern" later occupies various situations in the cell, but always remains as a small structure and does not enter into the construction of the spiral body of the sperm; it finally comes to lie in the cytoplasm which becomes attached, as a vesicle, to the posterior coil of the mature sperm.

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[2] Yamanouchi, Sh. Spermatogenesis, Oogenesis, and Fertilization in Nephrodium. *Bot. Gaz.*, XLV, p. 145, 1908.

Yamanouchi's results on Nephrodium are opposed to those of Belajeff for Marsilia, who holds that the blepharoplasts like centrosomes occupy the poles of the spindle and are derived from centrosomes in a previous mitosis within the antheridium. The account agrees with Webber's conclusions for Zamia that the blepharoplast arises *de novo* in the cytoplasm, and also with Shaw's view for Marsilia that the blepharoplast has no genetic relation to the pole of the spindle in the final mitosis.

It seems probable that the centrosome theory of the blepharoplast, as held by Belajeff, Ikeno and others, has placed undue emphasis on the proximity of the blepharoplasts, in the types studied, to the poles of a closely associated mitosis. There are no mitoses present during the entire period of zoospore formation in Derbesia, which consequently offers important evidence against this view. Since similar conditions are also present during zoospore formation in Œdogonium and a number of other algæ, the investigation of these types is likely to prove very interesting. The blepharoplast unquestionably gives a marked polarity to the cell, but it has not yet been established that this polar organization is derived, as such, from the immediate cell progenitors, however pleasing, for theoretical reasons, would be the establishment of such a history.

BRADLEY M. DAVIS.

ORNITHOLOGY

Riddle on the Genesis of Fault-bars and the Cause of Alternation of Light and Dark Bars in Feathers.[1]—In a much shorter paper

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[1] Riddle, Oscar. The Genesis of Fault-bars in Feathers and the Cause of Alternation of Light and Dark Fundamental Bars. *Biological Bulletin*, Vol. XIV, No. 6, May, 1908, pp. 328–370, pls. xii–xv.